

NEW TRIASSIC ISOPOD CRUSTACEANS FROM NORTHERN ITALY

by DANIELA BASSO *and* ANDREA TINTORI

ABSTRACT. Two new Triassic isopod crustaceans from the southern Calcareous Alps are described on the basis of well preserved specimens. This small assemblage comes from the late Norian Calcare di Zorzino, which is especially well-known for its vertebrate fauna. At least two new genera of Isopoda are present, here assigned to the Sphaeromatidae and Serolidae. *Triassphaeroma magnificum* is erected for specimens whose single first pleonal unit comprises five fused tergites, a feature peculiar to Sphaeromatidae. *Elioserolis alpina* is the first definitive fossil representative of the Serolidae so far known; attribution is on the basis of the round shape, head inserted in the first pereonite, and reduced number of pleonites. Specimens are preserved in a way which indicates that the biphasic moulting of Recent isopods had already evolved in late Triassic serolids.

THE Calcare di Zorzino (Zorzino Limestone) of Lombardy, northern Italy, was deposited in an anoxic environment (Tintori 1992), and it has yielded an abundant, well-preserved fauna. Although fishes (about forty genera) and reptiles (more than ten genera) make up its bulk, invertebrates are also well represented. Crustaceans were among the first elements to be studied (Pinna 1974), but subsequent research has focused mainly on vertebrates (Wild 1978; Tintori 1983, 1992; Renesto 1994). Fieldwork and preparation of material are still in progress. Interesting new specimens, belonging to poorly known groups, are commonly discovered, such as the isopod crustaceans which are the subject of this paper. The good, sometimes three-dimensional preservation of several specimens has allowed a complete restoration of the dorsal exoskeleton of the sphaeromatid *Triassphaeroma magnificum* gen. et sp. nov.; and two flattened specimens are ascribed to the serolid *Elioserolis alpina* gen. et sp. nov. The Calcare di Zorzino yielded a further isopod taxon, represented by a single, poorly preserved specimen, which is not described here. It is rather long (somewhat less than 20 mm), with everted head, seven large pereonites and six small free pleonites. Uropod insertion is not visible, so we cannot give a confident attribution, but it seems to be closely comparable to oniscoidean isopods. All the specimens of *Triassphaeroma magnificum* are from a locality at Endenna, and the other specimens are from a nearby locality designated 'Zogno 2'.

GEOLOGICAL SETTING, PALAEOENVIRONMENT AND TAPHONOMY

The Calcare di Zorzino is considered to be of middle-late Norian (Late Triassic) age, mainly on the basis of its stratigraphical position. It is coeval with the topmost part of the Dolomia Principale, a carbonate platform extending from Spain to Greece (Jadoul *et al.* 1992). The fossiliferous beds lie in the uppermost part of the Calcare di Zorzino and, based on evidence from the evolution of *Samrichthys* (Tintori 1990), they are dated around the boundary between the Alaunian and Sevatian (middle-late Norian).

The Calcare di Zorzino was deposited in basins which were probably a few hundred metres deep in their centres, where they were anoxic (Jadoul 1986; Jadoul *et al.* 1992), and had shallow margins of variable width, where the water was oxygenated (Tintori *in press*). An invertebrate fauna thrived along these margins, dominated by bivalve molluscs (mainly *Modiolus* and *Isognomon*) and crustaceans (Pinna 1974). Gastropods, echinoderms, brachiopods and corals were also present, but are rarely represented in the fauna. In order to be fossilized, the remains of all these organisms had

to be transported to the anoxic portion of the basins; otherwise, they would have been destroyed by the dolomitization that affected the shallow-water sediments in the area where they are inferred to have lived. From the shelled invertebrates, as well as from the durophagous vertebrates that fed on them (Tintori in press), we can infer that the oxygenated margins of the basins, up to a depth of 20–30 m, supported the richest benthic community. But since all of the fossils are found in the anoxic sediments, they must be considered as allochthonous.

Two main benthic environments can be distinguished: a rim of small patch reefs and organic mounds that bordered the basins (Jadoul *et al.* 1992) and, towards the basin centre, a muddy-bottomed area, colonized by the bivalve fauna. Specialized durophagous and semidurophagous fishes (Tintori in press) probably fed on the bivalves, picking them up with their anterior chisel-shaped or elongated teeth and crushing the shells with their stout, inner dentition.

Hard and soft substrates were both available to small organisms such as isopods. Living sphaeromatid isopods are widespread in brackish to marine waters, down to a few metres depth. They are usually associated with sea-weeds, barnacles or mussel beds, which provide shelter against wave and current action (Naylor 1972). For further protection, sphaeromatids are usually capable of enrollment. Living in rough surfaced environments, their dorsal exoskeleton is often well ornamented (Dumay 1971). Thus, the environments occupied by sphaeromatids today are very similar to those inferred to be present along the margins of the Norian basin, especially the shallow-water mussel beds.

By analogy with living species, the functional morphology and poor mineralization of the exoskeleton of the fossil Serolidae suggest a soft-bottomed, low energy habitat. Thus, *Elioserolis* probably inhabited a deeper and quieter area than the mussel community.

The Norian fauna is usually very well preserved; almost all vertebrate and arthropod specimens are complete and fully articulated (Tintori 1992). Only in a few cases are distal parts missing, owing to post-mortem transport.

Because the sphaeromatids are complete, at least in the dorsal exoskeleton, they may have reached the anoxic area whilst still alive. Alternatively, since appendages are not visible in most of our specimens, they might be exuviae. In this case, these may have sunk into the anoxic waters after transport over a short distance by very weak currents. Biphasic moulting, which is typical of many isopods (George 1972), is evident in *Elioserolis*, as shown by the peculiar aspect of both specimens. Both show a much more mineralized anterior (head plus the four anterior pereionites) than posterior region (the three posteriormost pereionites and the pleonites). Since head and appendages are all present, specimens are thought to be dead individuals rather than exuviae. Thus, they possibly died during moulting, just after shedding the old dorso-posterior region of the exoskeleton. *Triassphaeroma* does not show any evidence of biphasic moulting.

On some specimens the original microstructure of the exoskeleton of *Triassphaeroma* is well preserved. Both micro- and macro-ornamentation are shown (Text-fig. 2A–C). In a few specimens, the inner side of the dorsal exoskeleton is visible, but shows little detail. Specimens preserved in marly limestone are very thin, but show impressions of appendages. *Elioserolis* and the undetermined specimen from locality 'Zogno 2' are also preserved as thin, organic films on the lamina surface.

SYSTEMATIC PALAEOLOGY

Class MALACOSTRACA Latreille, 1806

Superorder PERACARIDA Calman, 1904

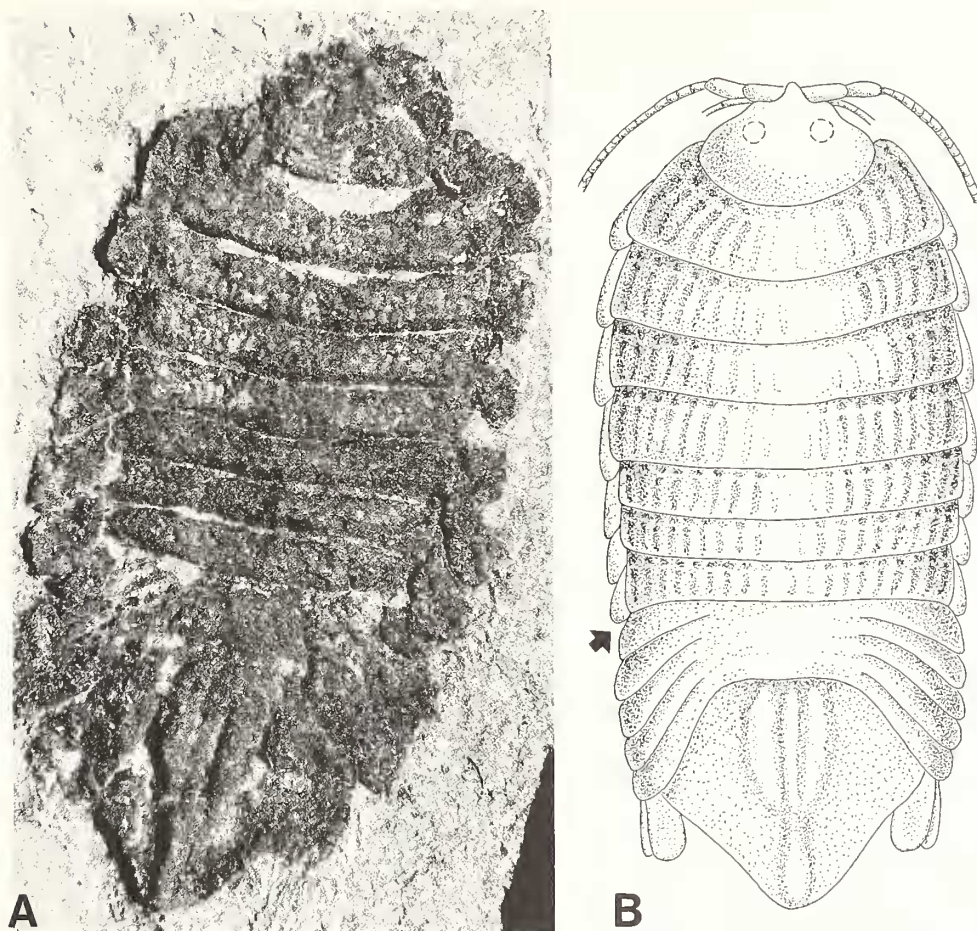
Order ISOPODA Latreille, 1817

Suborder FLABELLIFERA Sars, 1882

Family SPHAEROMATIDAE H. Milne-Edwards, 1840 [*nom. correct.* Dahl, 1916]

Genus TRIASSPHAEROMA gen. nov.

Derivation of name. From the age of the fossil material combined with the name of the living genus.



TEXT-FIG. 1. *Triassphaeroma magnificentum* gen. et sp. nov. A, MPUM 6692, holotype; Calcare di Zorzino (Triassic, Norian); Endenna, Zogno, Bergamo, northern Italy; note the antennae bases, the macroornamentation, the first pleonal unit showing traces of segmentation and longitudinal ridges on the pleotelson; $\times 15$. B, restoration in dorsal view; the arrow points to the boundary between the pereion and the pleon.

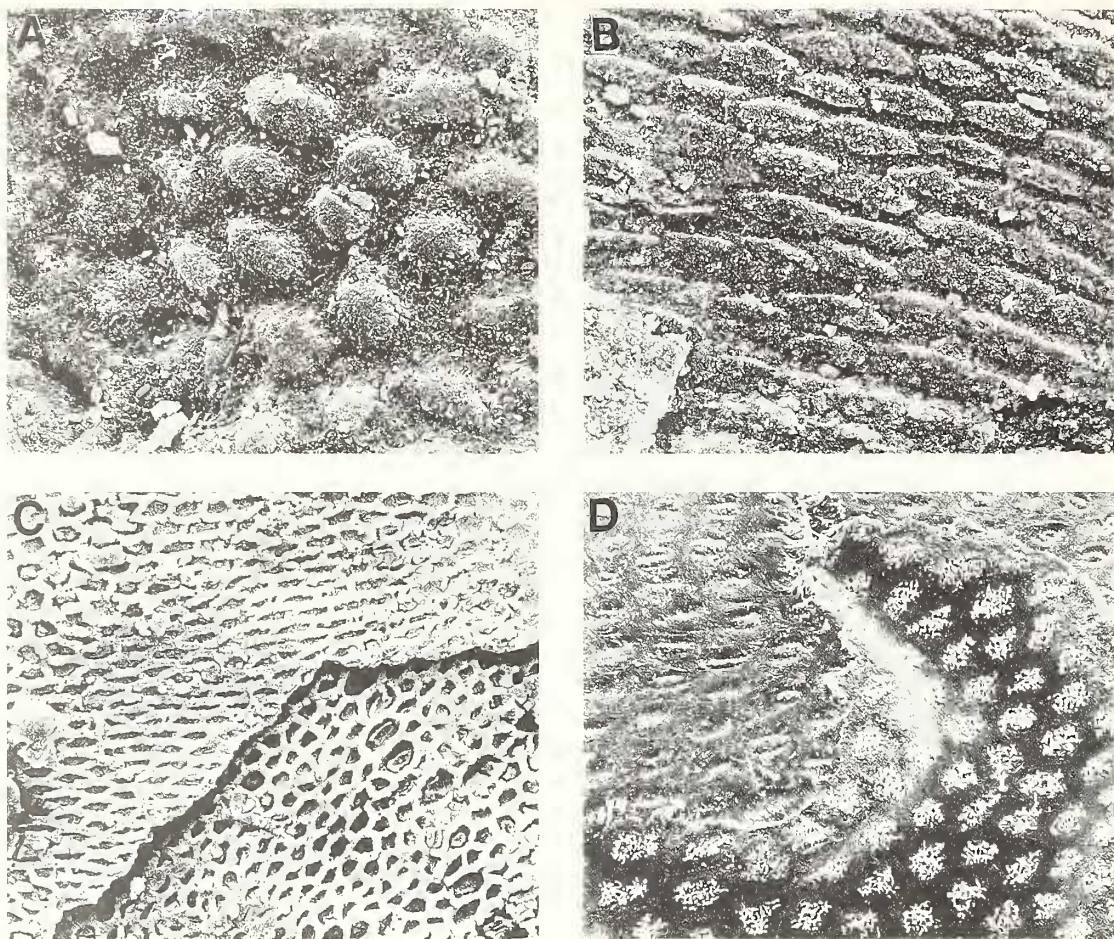
Diagnosis. Body ovoid, about three times as long as wide (pereionite width); cephalon as long as the first pereionite, in which it is partially sunken, but narrower (width about 65 per cent of the first pereionite); pereionites ornamented with pits and longitudinal furrows; epimeres well defined, transversely elongated, rhomboidal; anterior unit of pleon made up of five fused pleonites with suture lines only on the lateral regions; subtriangular telson rather pointed with median and lateral longitudinal ridges, each bearing a large tubercle; biramous, smooth-edged uropods about two-thirds the length of the telson; pereionites ambulatory.

Triassphaeroma magnificentum sp. nov.

Text-figures 1, 2A-C

Derivation of name. Latin, *magnificum*, reflecting the fine preservation of most specimens.

Types. The holotype MPUM 6692 (Palaentological Museum of the Università degli Studi di Milano) and seventeen paratypes (MPUM 6693-6707 and MPUM 7034-35). Three specimens have counterparts.



TEXT-FIG. 2. A-C, *Triassphaeroma magnificum* gen. et sp. nov. Calcare di Zorzino; Endenna, Zogno, Bergamo, northern Italy; A, details of micro-ornamentation in the anterior region of a pereiopod; MPUM 6706; $\times 1700$; B, details of micro-ornamentation in the posterior region of a pereiopod; MPUM 6706; $\times 1100$; C, details of cuticular microstructure; note the double reticulate sheets; MPUM 6707; $\times 500$; D, *Cymodoce* sp. Pontian Archipelago, western Mediterranean, at 69 m depth; details of cuticular microstructure; cavities in the reticular pattern are occupied by chromatophores; $\times 750$. All scanning electron micrographs.

Preservation depends on the lithology: in dark grey limestone the shape of the body and the morphology of the somites as well as their ornamentation are clearly evident. The specimens found in light brown marls show traces of the appendages. All from Calcare di Zorzino, Endenna, Zogno near Bergamo, northern Italy.

Diagnosis. As for genus.

Description. The body is oblong-ovate, two to three times as long as wide. The mean length is 8.5 mm (minimum 6.9 mm, maximum 10.8 mm), and the mean width, measured at the widest point, is 4.7 mm (minimum 3.0 mm, maximum 6.5 mm). The head is wider than long (3:2), with the anterior margin produced at the median point, over the base of the antennae, which have a multiarticulated peduncle and a flagellum composed of at least fourteen articles, reaching the posterior margin of the first thoracic tergite. The antennules and the eyes are unknown. The first tergite of the pereion is the longest, tergites II to IV are shorter and

subequal, tergites V to VII are the shortest and again subequal. The epimera are large, rhomboidal and clearly distinct from the tergites. They point backwards, extending beyond the postero-lateral angle of their respective tergites. However, the first one reaches only to the posterior edge of its tergite. The last two epimera are posteriorly more rounded than the others. The pereopods are ambulatory. The pleon is formed by two units, the first of which is as long as the first pereonite and shows four suture lines in the lateral regions. Lateral ends of this anterior unit project backwards and reach half the length of telson. The telson is usually subtriangular with a rounded posterior tip. A median ridge is present; it widens in the posterior third of the telson itself, expanding into a tubercle. Two large, elongate elevations flank the anterior part of the median ridge. Each also bears a tubercle at the posterior end. The uropods are biramous, the two branches of equal length. They are shorter than the telson, reaching about the posterior third, and have smooth margins and a rounded apex. The uropodal exopod is narrower than the endopod.

In a few specimens the shape of the telson is slightly different, being more rounded, without a protruding posterior tip; the ridges are less evident and the whole surface is covered by several relatively large pits. The uropods are somewhat longer. Differences detected in the telson shape and ornamentation may be interpreted as due to sexual dimorphism, even though this is not common in extant sphaeromatids.

Each thoracic tergite shows a row of about twenty round pits near the anterior margin. Behind each pit, there is a longitudinal depression, which does not reach the posterior edge. A few scattered shallow, round depressions are present on the telson. The whole surface of the body bears a fine micro-ornamentation (Text-fig. 2A–B). The shape of the microtubercles varies, relative to the position on each single pereonite: the anterior part is covered by domed, round granules, while the posterior one bears flat, transverse elements.

The cuticle is composed of two reticulate sheets (Text-fig. 2C) whose meshes can vary in shape from polygonal to very elongate.

Discussion. Among the several characters diagnostic for this family, only the pleon structure is easily detected on fossil material. The pleon itself is made up of only two units, the first formed by the fusion of the five anteriormost pleonites. In modern genera, three transverse sutures are usually present on this element, often only in the lateral regions (Naylor 1972). Because our specimens show clearly a single anterior pleonal unit, with four incomplete suture lines, we are confident that they belong to the Sphaeromatidae. Furthermore, we compared the microstructure of one of our specimens to that of an extant sphaeromatid (*Cymodoce*), and a few other isopod genera belonging to the Cirolanidae (*Cirolana* and *Aega*) and Gnathiidae (*Gnathia*). Similarities between *Triassphaeroma* and *Cymodoce* are striking, both showing an inner lattice of skeletal material (Text-fig. 2C–D). The other genera studied have a smooth or punctate surface, as observed by Wieder and Feldmann (1989) in the cirolanid *Palaega* Woodward, 1870 (= *Bathynomus* Milne Edwards, 1879), but have a fibrous inner structure.

Even if phylogenetic relationships with Recent sphaeromatid genera cannot properly be established, we find close affinities between our new genus and the extant genera *Sphaeroma* Latreille, 1804 and *Exosphaeroma* Stebbing, 1904, especially in the shape of pleotelson and the size of uropod. Fossil species placed in *Sphaeroma* are too poorly preserved, or show details of the pleotelson that do not allow their attribution to the genus (Van Straelen 1928). A few fossil genera are known; following the suggestion of Hessler (1969, p. R374), we compare our Triassic material mainly with them.

Isopodites von Ammon, 1882, is the only other sphaeromatid-like isopod from Triassic strata. It is very different from all other genera in having a very elongate cephalon. The short first pleonal unit with no traces of sutures, and the thin uropods which are much longer than the telson, are further characters distinguishing *Isopodites* from our specimens. *Eosphaeroma* Woodward, 1879 (from the Oligocene) is the fossil genus closest to our material in morphology. According to Van Straelen (1928) *Eosphaeroma* can be considered a 'basket genus' for the sphaeromatid-like isopods from the Cainozoic. Apart from differing in age from the new material (which is of limited significance in such a slowly evolving group), *Eosphaeroma* is very different in most diagnostic characters useful for the palaeontological taxonomy of this group; these are cephalon shape and dimensions, first pleonal unit structure, shape of the telson and relative length of uropods. All other fossil genera are very distinct from *Triassphaeroma* in shape and body proportions (Hessler 1969; Iverson and Chivers 1984).

Family SEROLIDAE Dana, 1852

Discussion. Fossil serolids are very rare: apart from *Elioserolis* gen. nov., only *Anhelkocephalon* tentatively can be ascribed to this family (Schwebel *et al.* 1983) on the basis of the enlarged telson, as suggested by Bill (1914), whose description of *A. handlirschi* was based on specimens from the Triassic Voltzia Sandstone of the Vosges. However, neither a diagnosis or an illustration was given. Bill (1914) erected his taxon on the following characters: cephalon deeply embedded in the first pereonite, a reduced number of pleonites, and a large telson. On this basis *A. handlirschi* is only identified as a serolid-like isopod. Von Straelen (1928) was unable to locate the holotype at the Institut de Géologie de Strasbourg, and doubted if *A. handlirschi* should be included in the Serolidae. According to Schwebel *et al.* (1983), Bill's specimens were lost in a fire at the institute in 1967, and they redescribed the species using new material and selected a neotype. The latter is 30 mm long, while a second specimen is less than 8 mm long; both are known only from the ventral side. The main difference from the original description (Bill 1914) concerns the head; in ventral view 'le cephalon paraît nettement dégagé du pereion' (Schwebel *et al.* 1983, p. 308). However, we cannot exclude the posterior dorsal fusion of the cephalon with the first pereonite, so that the old (Bill 1914) and new (Schwebel *et al.* 1983) descriptions may be compatible.

Because Bill's specimens were in dorsal view, and those of Schwebel *et al.* are both in ventral view, a confident attribution of the latter to Bill's species is difficult, because characters visible on the dorsal and ventral sides cannot precisely be related to each other. However, since all the material comes from the same horizon, it could well belong the same taxon. Bill's vague original description of *A. handlirschi* easily encompasses our fossils, but this is not the case for the neotype of Schwebel *et al.* (1983). The telson proportions of the latter are very different from our material, as well as from those of all living serolids.

Hessler (1969, p. R379) gave the following diagnosis for the Serolidae (here quoted only for characters usually visible on fossil material): 'body strongly flattened and broad, cephalon sunk deeply into first pereonite and fused to it posteriorly; antennules and antennae both with well-defined peduncle and multiarticulate flagellum; epimeres of pereonite extensive; tergum of last thoracomere usually absent; pleon composed of four units, three relatively subequal pleonites and one large pleotelson; uropoda lateral, with free rami'.

More recently, Brandt (1988) gave a different interpretation of the dorsal segmentation of serolids, considering the reduced element once regarded as the first pleonite (Richardson 1905; Hessler 1969) to be a seventh pereonite. We are not convinced by this change of interpretation of living serolids; even early authors should not have had difficulty in finding the correspondence between thoracic limbs and tergites. A full review of this apparent contradiction is beyond the scope of this work; however, we must point out that in many other isopods the first pleonite appears dorsally reduced in the central region and laterally surrounded by the last pereonite, which is always complete in its lateral regions. Furthermore, in many serolids the last one or two 'complete' pereonites (*sensu* Brandt 1988) show a great reduction in the median region (see, for instance, *Heteroserolis australiensis* (Beddard, 1884) or *Frontoserolis waegelei* (Brandt, 1988)). An inversion of this reduction tendency in the last (seventh) pereonite (*sensu* Brandt 1988) seems very unlikely. Brandt (1988) also noted that in serolids the first three pleopods are similar; thus they would more likely belong to three free pleonites rather than to two as in Brandt's interpretation. The biphasic moulting recorded in *Elioserolis* gen. nov. also points to the presence of seven completely developed pereonites. In the light of these remarks, and from a palaeontological point of view, we prefer to follow Hessler's interpretation, considering the pleon comprising three free pleonites followed by a pleotelson.

However, the statement concerning the lack of the seventh pereonite on the dorsal side (Hessler 1969) seems to be in contrast with the clear evidence of seven complete and distinct thoracic tergites in some Recent species, as well as in our Triassic specimens. In Recent serolids, the first two tergites appear to be firmly fixed to each other or fused together, but with more-or-less evident suture lines, so that they are usually considered as one unit. In her diagnosis of *Ceratoserolis* Cals, 1977, Brandt

(1988, p. 34) wrote: 'Mediolaterally of head on both sides a shallow suture running almost parallel to the caudal margin of the first pereionite' and illustrated this feature in *Ceratoserolis pasternaki* (Kussakin, 1967) and *Serolis aestimabilis* Brandt, 1988.

In our interpretation, the seventh tergum does exist, the reduction (fusion) taking place in the two most anterior ones. The Triassic specimens show seven pereionites, as in our interpretation of Recent *Serolis*, but they are all completely free. We regard this as a reflection of the relative primitiveness of *Elioserolis* gen. nov. compared to *Serolis* s.l. This is in agreement with the general evolutionary trend of Crustacea toward a reduction of the number of free thoracic segments. Thus, we feel confident that *Elioserolis* gen. nov. can be ascribed to Serolidae, in spite of its free first two pereionites. We therefore emend Hessler's (1969) family diagnosis, as it applies to the number and development of the pereionites, as follows: Serolidae showing seven complete pereionites, at least in the lateral regions; the first two may be free or fused with a more or less visible suture.

Genus ELIOSEROLIS gen. nov.

Derivation of name. For Professor Elio Robba, Università degli Studi di Milano, with the suffix *serolis*.

Diagnosis. Medium-sized (up to 12 mm) serolid; body outline broadly oval; cephalon deeply embedded in the first pereionite (dorsal view); pereionites with obtusely rounded antero-lateral angle, well protruded postero-lateral ends and triangular expansion in the middle of lateral posterior edge; three pleonites, the first of which is reduced; subtriangular telson.

Elioserolis alpina sp. nov.

Text-figure 3

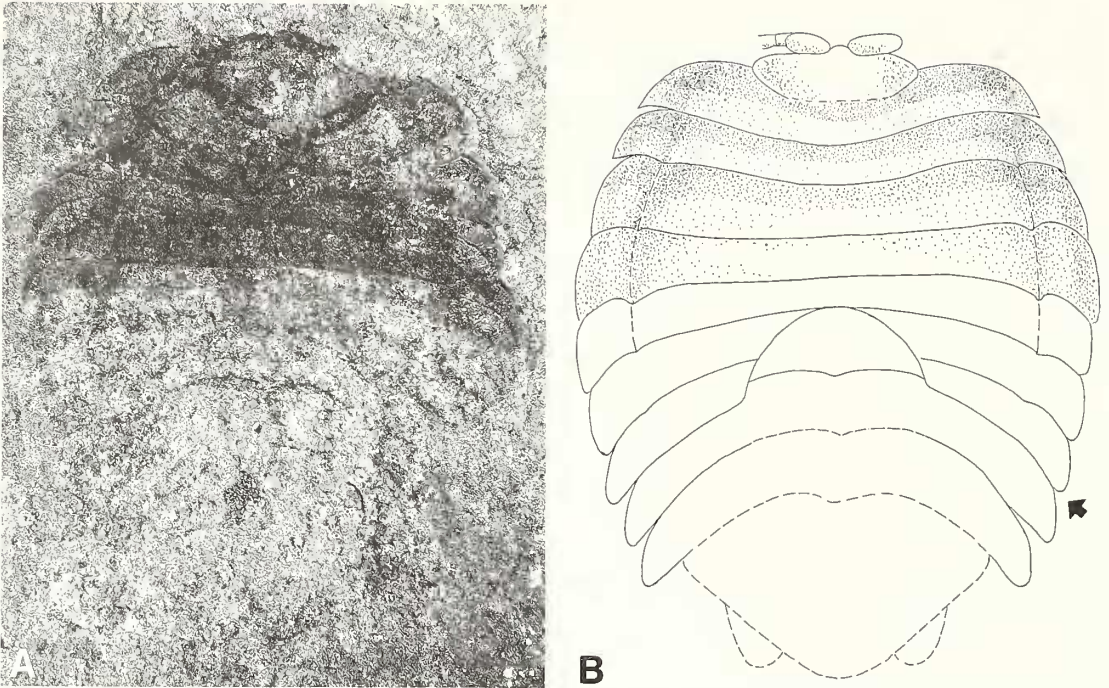
Derivation of name. From the Alps, where the specimens were found.

Types. Holotype MPUM 7036 in dorsal view, part and counterpart; paratype MPUM 7037 in ventral view, incomplete on its left side. The only other known specimen. Both from Calcare di Zorzino, Zogno 2, Bergamo, northern Italy.

Diagnosis. As for genus.

Description. Body broadly oval, narrower than long, the holotype being 11 mm long and 9 mm wide. The second, incomplete, specimen is somewhat larger. The cephalon is hardly distinguishable from the pereionite in which it is sunken. The antennae are articulated, with the first article of the peduncle about 0.5 mm long. The preserved part of the peduncle itself is about three times as long as wide. Only three flagellum articles are visible on the left antenna. The pereion shows seven somites, the first of which encircles the cephalon. The following four are similar, while the seventh is greatly reduced in its median region, where it appears to be fused with the sixth. Pereionites are dorsally expanded, the coxal plates being fused to the corresponding tergite. The antero-lateral angles of each pereionite are obtusely rounded, while the postero-lateral ends project backwards. The posterior edge of the first three pereionites shows a small, triangular expansion near the insertion of the coxal plates. The mineralization is markedly lighter in pereionites V–VII. All pereionites are divided transversely by a thin line marking a slight difference in mineralization between the anterior and posterior part. In the first three pereionites this line runs parallel to their posterior margin. Posterior to the pereion, three short pleonites are visible, the posterior two with well-developed epimeres. The first pleonite is reduced in the central region, as in modern serolids, and also shows a posteriorly directed median tip. The other two are complete. The light mineralization prevents a clear view of the pleotelson region, but traces of a fourth pleonal segment are still visible in the lateral region, perhaps partially fused to the pleotelson itself, as is the case in modern serolids. The pleotelson seems to be subtriangular, with a rounded posterior tip. Legs are robust and ambulatory, with dactylus curved and much thinner than propodus. All leg podomeres bore dense setae.

Mineralization of both specimens is heavy in the anterior region (head and the four anteriormost pereionites) whereas it is very light in the last three pereionites and the pleon. As suggested above, this can be related to the biphasic moulting which occurs in most isopods (George 1972). As George (1972) pointed out, the ecdysis



TEXT-FIG. 3. *Elioserolis alpina* gen. et sp. nov. A, MPUM 7036a, holotype; Calcare di Zorzino; Zogno 2, Bergamo, northern Italy; note the much more mineralized anterior region showing four free pereonites and the crescentic reduced first pleonite; $\times 10$. B, restoration in dorsal view; the arrow points to the boundary between the pereon and the pleon.

of the posterior half (the three posteriormost pereonal somites plus the pleon) precedes that of the anterior. Thus, two-phase moulting had already evolved by Triassic times, at least within serolids.

CONCLUSIONS

Although caution is needed when comparing fossil and living species (Hessler 1969), strong similarities have allowed the new Triassic isopods to be assigned to Recent taxa, at least at supra-generic rank. *Triassphaeroma magnificum* belongs to the Flabellifera, a group encompassing several fossil taxa. Our material can confidently be ascribed to the Sphaeromatidae on the basis of both morphological analogies and exoskeletal ornamentation and microstructure, the latter being the first described from fossil isopods.

The stratigraphical range of Serolidae is extended back to the Triassic; *Elioserolis* is the only definitive fossil representative of the family. Seven free and laterally complete pereonites are present, so that we can consider *Elioserolis* as the most primitive serolid, the extant ones showing different degrees of fusion of the first two dorsal segments. On the basis of this character, the diagnosis of the family Serolidae has been emended. A bi-phasic moulting style, as observed in most modern isopods, is also recorded. An analysis of evolutionary phenomena involved in the origin and dispersion of Serolidae has been given by Brandt (1992a, 1992b). She concluded that 'the centre of origin of the family lies in a cold-temperate Gondwana province' (Brandt 1992a, p. 419). She also hypothesized a shelf habitat for primitive species, while derived relatives appear to be distributed in the deep sea, thus providing evidence of an onshore-offshore migration. *E. alpina* inhabited a sub-tropical intracarbonate platform basin in western Tethys during the Triassic. Thus, the problem of localizing the centre of origin for the geographic dispersal of the Serolidae can be seen in a new

light. The family is much older than the previously supposed 90 Ma (Brandt 1992a), extending back for over 210 Ma.

Though no other fossil serolids are known in the interval between the Triassic and today, we can speculate that the primitive dispersal centre lay in westernmost Tethys, which had a rather warm environment. The opening of the central and southern Atlantic during Jurassic and Cretaceous times may have led serolids to migrate southwards along the continental shelf of South America, from warm to cold waters. They could have colonized the southernmost region of the Atlantic before South Africa separated from the block comprising South America, Antarctica and Australia, supporting the present day, mainly southern, distribution. Thus, serolids in the Caribbean region could be regarded as a relict primitive population rather than a recent immigration from Antarctica as suggested by Brandt (1992a).

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DANIELA BASSO

ANDREA TINTORI

Università degli studi di Milano
Dipartimento Scienze della Terra
Via Mangiagalli, 34
20133 Milano, Italy

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